The following papers were read :---

1. A Contribution to the Skeletal Anatomy of the Frilled Shark, Chlamydoselachus anguineus Gar. By T. GOODEY, M.Sc. (Birm.), Research Scholar, University of Birmingham \*.

[Received February 14, 1910.]

(Plates XLII.-XLVI.<sup>+</sup>)

### CONTENTS.

1. Introduction.

II. Measurements.

III. The Skull, Visceral and Branchial Arches.

a. Cranium.

b. Labial Cartilages.
c. First and second Visceral Arches, Ligaments and Muscles,
d. Branchial Arches.

e. Branchial Rays.

- f. The Spiracle.
- g. Features of specialization and comparison with Notidanidæ.

IV. The Membranous Labyrinth.

V. The Vertebral Column.

- h. Description of regions 1, 2, 3, & 4.
- i. Summary of special features and comparison with Notidanidæ.

VI. The Pectoral Girdle and Fin.

VII. The Pelvic Girdle and Fin in the female.

VIII. The Mixipterygia (Copulatory Appendages).

- *j*. Measurements. *k*. Externals. *i*. Musculature.

- m. Skeleton.

IX. The Median Fins.

X. Summary.

XI. Literature.

XII. Explanation of Plates and Reference Letters.

### I. INTRODUCTION.

The present paper is the ontcome of a piece of research, carried out in the Zoological Laboratory of the University of Birmingham, on the skeletal anatomy of the primitive Selachian Chlamydoselachus anguineus.

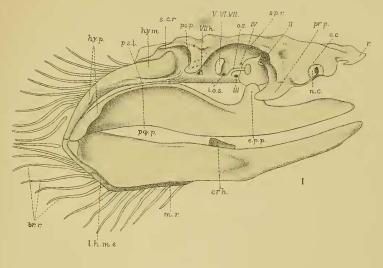
The work was suggested by the late Prof. Bridge, and a large part of it, that dealing with the skull and vertebral column, was carried out under his supervision. I should like here to say how much I appreciate the opportunity of using such valuable material, and to express my gratitude for the helpful criticism which my late teacher was always willing to give. The material included one perfectly complete male specimen, the greater part of a large female specimen, and the remains of another male, which was principally in the form of parts set up as museum specimens.

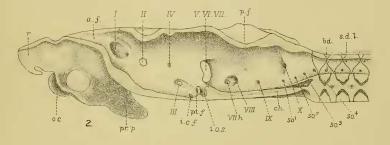
\* Communicated by Dr. P. CHALMERS MITCHELL, M.A., F.R.S.

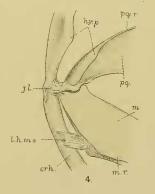
+ For explanation of the Plates sec page 570.

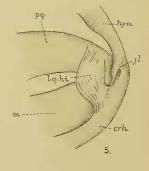
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P. Z.S. 1910 P1 XLII.



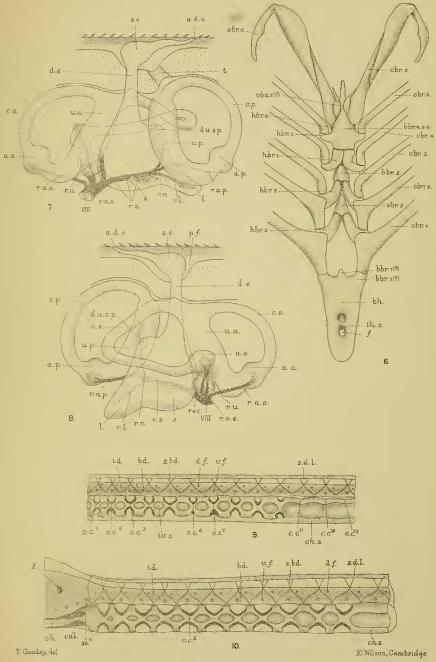






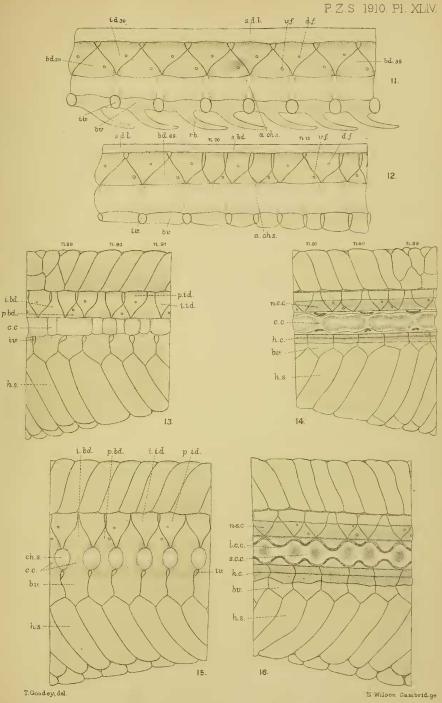
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E.Wilson, Cambridge. CHLAMYDOSELACHUS ANGUINEUS Gar .

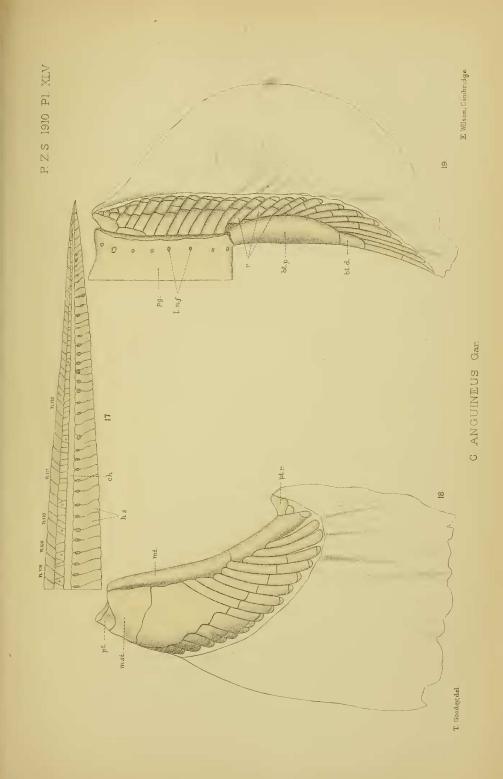


C. ANCUINEUS Gar

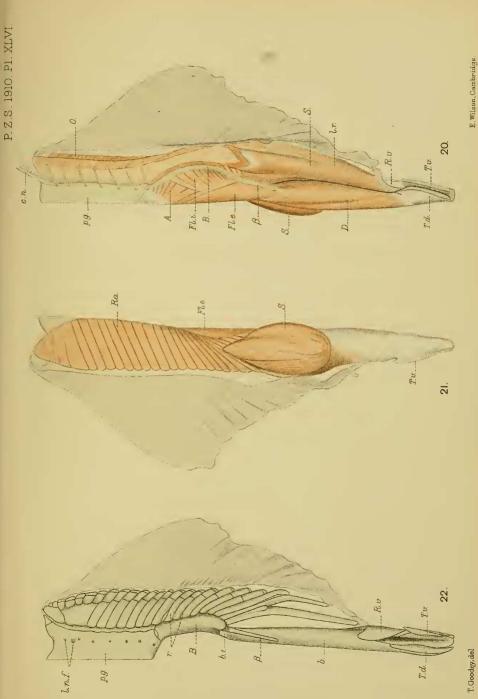




C. ANGUINEUS Gar.







C. ANGUINEUS Gar



There are several reasons why a detailed knowledge of this fish is especially desirable. In the first place, Chlamydoselachus anguineus is admittedly a primitive member of the Selachian group of fishes, and by virtue of its position, it demands a more considerable knowledge of its structure and anatomy than would be the case were it a member of one of the higher and more specialized groups of Selachians. Furthermore, the original account of the fish given by Garman (10) is in many parts very limited and indefinite, whilst the figures are rather indistinct and in a few cases inaccurate. Little work has been carried out on the anatomy of the skeleton since the publication of this paper. Günther (14) has dealt with the skeleton of the mixipterygia and with the abdominal viscera. Braus (2 & 3) has dealt with the pelvic plexus in the earlier of the two papers, and in the second one has given a short comparative account of the pectoral girdle and fin and of the mixipterygia. Fürbringer (6) has described the labial cartilages and the vestigial seventh branchial arch, which were not discovered by Garman.

In addition to these, there is a paper by Ayres (1) on the comparative anatomy of the arterial system, and two papers by Hawkes (16 & 17), the first on the cranial and spinal nerves, and the second on the abdominal viscera and the vestigial seventh branchial arch.

My best thanks are also due to Prof. Gamble for many helpful suggestions during the progress of the work since the death of Prof. Bridge.

### II. MEASUREMENTS.

I give certain measurements which may be of service as indicating the size of the specimens examined and also as perhaps denoting in an indirect way their comparative age.

Total length, 52 ins. (Garman's specimen 59.5 ins. Günther's 58 ins.).

,, to end of gill-covers   7.7 ,,     ,, to end of left pectoral fin   11 ,,     ,, to base of pelvic girdle   25.5 ,,     ,, to anus   27 ,,	Snout to angle of mouth	3.5	ins.
", to base of pelvic girdle		7.7	,,
, to anus	, to end of left pectoral fin	11	,,
,, to anus	,, to base of pelvic girdle	25.5	17
		27	
, to base of anal fin $\dots 31.8$ ,	,, to base of anal fin	31.8	
, to end of anal fin	, to end of anal fin	38.8	
, to base of dorsal fin $\dots 32.5$ ,	, to base of dorsal fin	32.5	
", to end of dorsal fin		38	
Greatest depth of caudal fin 3.7 "	Greatest depth of caudal fin	3.7	
Width across anal and dorsal fins 4.8		4.8	
Width across eyes 2.8 "	Width across eyes	2.8	

### Tail of large female specimen referred to in paper.

Length of tail from root of caudal fin to tip	18 ins.
Greatest depth of caudal fin	5 .,

# III. THE SKULL, VISCERAL ARCHES, ETC. (Plates XLII., XLIII. figs. 1-6.)

My observations on two skulls agree in the more important points with the description given by Garman (10) pp. 7–9. It is not my intention in the present account to redescribe the whole of the structure, but rather to amplify the original description in those points which appear to call for special emphasis, and to make certain additions. I propose to deal first with the cranium, then with the first and second visceral arches and their ligaments, and finally with the branchial skeleton and certain other points.

### a. Cranium (fig. 1).

At the extreme anterior end of the cranium is the broad, flat, and somewhat rounded rostrum (r.), which is notched at its sides. Its shape gives to the nasal region a curious truncated appearance. The olfactory capsules (o.c.) are large, rounded, and thin-walled. Their large apertures have the nasal cartilages (n.c.)fitting into them. Each of these is ring-like and has a bar across the middle of the aperture so as to give rise to the double opening which each capsule presents in external appearance.

The anterior fontanelle (a.f.) is very large and broad, extending posteriorly to a point almost level with the preorbital process. Immediately behind the olfactory capsule is a deep furrow which communicates above with the foramen transmitting the ophthalmicus branch of the seventh nerve, and in which are found branches of the latter nerve. Posterior to this furrow is a somewhat prominent ridge having a sharp edge orbitally, and gradually running into the tapering backwardly directed preorbital process below. On the anterior side of the orbit is a very smooth, hollow surface, against which the eyeball rolls. On the cranial wall at the anterior end of the orbit is developed a rather prominent articular surface which receives the inner side of the ethmopalatine process of the palatoquadrate cartilage.

The supraorbital ridge is somewhat thin and prominent. In the shallow groove along its dorsal surface are a number of foramina which transmit branches of the ophthalmicus branch of the seventh nerve supplying the supraorbital sensory canal.

Garman described the postorbital process (po.p.) as of irregular shape and moderate breadth. In the specimen which I have examined it appears to be quite regular in outline. It is a backwardly curved, stoutish process, gradually tapering towards its rounded end. On its upper surface are found a number of foramina which also transmit branches of the seventh nerve to the sensory canal-system.

From the median vertical longitudinal section of the cranium (fig. 2), it is seen that the notochord is continued as a thin strand of tissue in the basis cranii as far forward as the pituitary fossa.

The cartilage of the floor of the cranium in the region of its junction with the vertebral column is thick and somewhat heavily calcified. It here shows some indication of its probable vertebral nature, by the slight resemblance which the calcification presents to the inverted V-formation found in the centra of the vertebral column.

The nerve foramina, as seen both from the inside and from the outside of the skull, deserve some consideration. The foramen for the first nerve (I.) is very large and lies just below the opening of the anterior fontanelle. The optic nerve foramen (II.) is moderately large and, seen from the inside, lies a short distance posterior to the opening for the olfactory nerve. On the outside it opens into a deep channel on the anterior dorsal side of the smooth articular surface which receives the ethmo-palatine process of the palatoquadrate. It is thus situated comparatively far forward in the orbit.

The foramen for the third nerve (III.) lies at the end of a forwardly curved groove on the inside of the skull. Externally it is placed close to the floor of the cranium just behind the posterior ridge of the above mentioned articular surface.

The aperture for the fourth nerve (IV.) is small and lies well up in the orbit, almost vertically above (III.). Behind foramen III. is the cartilaginous optic stalk (*o.s.*), against the expanded end of which the back of the eyeball rests. Immediately posterior to the origin of this stalk is a fairly large foramen which transmits the interorbital blood-sinus. On the inside of the skull, it is divided by means of a thin, outwardly directed cartilaginous bridge. The interorbital sinus passes posterior to this, whilst the cavity anterior to it forms the pituitary fossa. The foramen of the internal carotid artery (*i.c.f.*) is a small aperture lying in the floor of the skull immediately anterior to the pituitary fossa.

Nerves five, six, and seven are transmitted by a very large foramen (v. vi. & vii.) which is about twice as long as broad, and has a thin, backwardly directed ridge on its anterior edge. Following this is a double foramen (vii. & viii.) on the inside of the skull, which transmits the hyoidean branch of the seventh nerve and also nerve eight. The hyoidean part is the anterior smaller portion, which is continued directly outwards and opens externally just beneath the postorbital process. The foramen for nerve nine is small and is somewhat ventrally placed a short distance posterior to foramen viii. It is continued obliquely under the auditory capsule and opens externally at the back of the cranium in a very deep depression, overhung by the occipital ridges.

The tenth foramen is moderately large and on the inside is situated in the median line. It opens externally at the back of the skull just above the aperture for the ninth nerve. There are four small foramina, somewhat ventrally placed, the first one lying immediately below foramen x. These are the foramina of the spino-occipital nerves,  $so^{1}-so^{4}$ .

## b. Labial Cartilages.

These were not found by Garman, but Fürbringer (6) has described and figured them, and my observations agree well with his. On each side of the head there are three small, rod-like cartilages, two dorsal and one ventral to the mouth. The ventral one is the longest and meets the posterior dorsal one at the point of the angle of the mouth where both are united by ligament. The dorsal one of this pair is about two-thirds the length of the ventral one and is somewhat inwardly directed. The anterior dorsal one is distinct from those just described. It lies at the posterior end of a ligament which stretches beneath the orbit from the outer ridge of the preorbital process to a point beneath the postorbital process. It is very thin and at its anterior end is also inwardly directed.

### c. First and Second Visceral Arches, Ligaments and Muscles.

The suspension of the jaws is hyostylic. At its proximal end the hyomandibular articulates with a rather deep concavity on the auditory capsule. As Garman has pointed out, this articulation does not take place with the whole of the head of the hyomandibular, the latter having an oblique disposition to the skull. Thus, only the knob on the posterior side is in contact with the skull, and between the projecting anterior knob and the concavity there is a thick pad of capsular ligament. Garman has also given an accurate description of the general shape and disposition of the hyomandibular. It is suspended in a backward and downward direction at an angle of about forty degrees from the skull by a strong ligament which has its origin on the ventro-lateral surface of the auditory capsule. The ligament is attached to this region for some considerable distance, and from here proceeds obliquely backward. It lies internal and ventral to the hyomandibular, to which it is attached on the inner side at about one-half the length of the cartilage from the skull. It is post-spiracular in position and corresponds with the inferior post-spiracular ligament found in the Common Dogfish, Scyllium canicula, as described by Ridewood (27). There is no pre-spiracular ligament in Chlamydoselachus, and I agree with Garman in not finding a spiracular cartilage, though Fürbringer (6) has described and figured as one a minute piece of cartilage which shows hyaline structure in microscopic sections. I have little to add to Garman's account of the upper and lower jaws; my observations confirm their shape and disposition as recorded by him.

The joint between these two cartilages is a very interesting one, and was not dealt with in the original description. It is visible only when the jaws are opened to their widest extent (fig. 3). There are two articulations, each of the cup and ball type, one on the outer and one on the inner side of the joint. On the outer or posterior articulation the quadrate forms a broad, rather flattened knob which fits into a slight concavity of the posterior and outer end of the mandible. The inner or anterior articulation is formed by a prominent rounded protuberance somewhat more than half the width of the one on the quadrate which projects upwards into a corresponding concavity or facet in the quadrate.

This joint affords a resemblance with Heptanchus, the corresponding joint in which has been worked out by Gadow (8). There is the difference, however, that in Chlamydoselachus it is much more pronounced and has not the space separating the two articulations found in Heptanchus. Garman mentions a palatal or trabecular process which occurs at a point an inch and three-quarters behind the front end of the palatoquadrate, and is received in a concave articular depression of the skull in the orbit. He says that it is attached at its upper end by ligament to the skull near the top of the orbital cavity. I have found the process in question in both skulls that I have examined. It is perhaps better to call it an ethmo-palatine process, this being in accord with modern nomenclature. I cannot, however, agree with Garman in what he says about its ligamentous attachment to the skull. It is not attached by any definite band-like ligament such as that figured by him on Pl. viii. It is surmounted by a pad of capsular ligament which appears to be in the nature of a thickening of the general soft connective tissue surrounding the whole process. A similar capsular ligament has already been described as occurring between the obliquely placed head of the hyomandibular and the articular concavity on the side of the Both are very different from the strong, auditory capsule. fibrous, band-like post-spiracular ligament which suspends the iaws from the skull.

I have found the hyal process which occurs on the upper ridge of the quadratic portion of the upper jaw, close to its posterior end, overhung by a similar one on the hyomandibular. The larger quadratic or otic process however, which, according to Garman, occurs farther forward at the widest part of the palatoquadrate, I have failed to discover.

The ceratohyals articulate by the anterior lobe of their lower extremities with the ventral surface of the basihyal, on either side of the median line. The latter cartilage is situated well forward between the mandibles and is raised up slightly into the oral cavity. As Garman has pointed out, it is elongate and tapers from the broader posterior end to the rounded anterior end. In the middle of the concave posterior border is a small, backwardly directed prominence, which Fürbringer (6) considers as the representative of the copula or basibranchial of the first branchial arch. The two lateral prominences, also at the posterior end, no doubt represent the hypobranchials of the first branchial arch as Garman suggested, and these together with the basibranchial have lost their distinct nature by becoming fused into the general mass of the basihyal.

On the ventral surface of the basihyal is found the somewhat PROC. ZOOL. Soc.—1910, No. XXXV. 35

oval excavation mentioned by Garman. In two cases out of three which I have examined, this communicates with the dorsal surface of the basihyal by means of a small round aperture at the anterior end of the concavity. In the third case, the excavation is not covered above by cartilage but was found to open directly into a slightly smaller concavity on the dorsal surface of the cartilage. The thyroid gland is situated in the bollow excavation on the ventral side, and in one example examined, a very interesting tubular structure, attached to the gland and communicating with the oral cavity, has been discovered. This is dealt with in a separate paper \*.

A strong ensheathing fibrous ligament wraps the inner side of the quadrato-mandibular joint. It is continued on to the outer side of the joint and then proceeds backward to wrap the distal end of the hyomandibular and the proximal end of the ceratohyal, both of which are somewhat closely applied to the jaw joint (fig. 4). It is by this ligament that the hypotylic suspension of the jaws is is brought about. The ceratohyal is very closely applied in the greater part of its length to the inner side of the mandible where it fits into a sort of shallow groove. It is held firmly in its position by means of two important ligaments, in addition to the one just described which connects its proximal end with the angle of the jaws. Of these two ligaments one is external and the other internal in position. The former stretches between a process on the outer ridge of the ventro-posterior side of the mandible and a corresponding ridge on the outer edge of the ceratohyal. It is about half an inch in width, and may be termed the ligamentum hyoideo-mandibulare externum. The inner one is a broad, flat ligament (fig. 5) attached at its upper end to the convex inner surface of the proximal end of the palatoquadrate cartilage, and, stretching across the jaw joint and the mandible, is inserted along the ridge on the inner and upper side of the ceratohyal. It may be termed the ligamentum quadrato-hyoideo internum.

The disposition of the head muscles has been dealt with by Fürbringer (6), but the more important ridges and processes on the skull and jaws, which serve for the attachment of these muscles, are also worthy of some attention, seeing that they are quite pronouncedly developed. It will perhaps be easier in dealing with these to take the muscles separately and describe their relations to the particular ridges of attachment.

Levator maxillæ is attached above to the thin ridge (s.c.s.) (t.in Garman, Pl. viii. fig. A) which projects over the auditory capsule, and to the posterior edge of the postorbital process. It extends in front of the spiracle and is inserted on the inner and upper edge of the prominent ridge (pq.r.) along the dorsal side of the quadratic portion of the palatoquadrate. This insertion extends as far backward as the hyal process.

\* Goodey, T., "Vestiges of the Thyroid in Chlamydoselachus anguineus, Scyllium catulus and S. canicula." Anatomischer Anzeiger, Bd. xxxvi. 1910.

Adductor mandibulæ is a thick massive muscle, filling up the concavities on the outer sides of the palatoquadrate and the mandible. It is divided by an aponeurosis, which is in the line of the mouth angle, and is attached above to the lower edge of the palatoquadrate ridge previously mentioned. Below, it is similarly attached to a correspondingly sharp ridge (m.r.) on the ventro-lateral border of the mandible.

Constrictor superficialis is a thin, extensive muscle lying behind the hyomandibular. It extends round the jaw angle to the ventral surface of the head, where it lies between the mandibles. It is attached above to the posterior end of the supra-capsular ridge (s.c.r.) and also to the outer surface of the hyomandibular. On the lower side it is attached to the inner edge of the sharp ridge (m.r.) which extends along the ventro-lateral border of the mandible.

### d. Branchial Arches (Plate XLIII. fig. 6).

Basibranchials.—The basibranchial of the first branchial arch is, as previously mentioned, probably represented by the median prominence (bbr. 1) on the posterior border of the basihyal. The second one (bbr. 2) is situated considerably posterior to the first, level, in fact, with the bases of the third ceratobranchials. It is triangular in outline, attached anteriorly to the second pair of hypobranchials (hbr. 2) and is free behind. The third (bbr. 3) is also triangular in outline and is distinct. It is attached by ligament anteriorly to the third pair of hypobranchials and is firmly united behind by ligament to the fourth pair of hypobranchials.

The fourth basibranchial is indistinguishable from the corresponding hypobranchials. Garman describes it as lying between these. However, in the two cases that I have examined it is certainly not present, and I am inclined to believe that it has become fused with the large posterior basibranchial. The latter no doubt represents the fourth, fifth, and sixth basibranchials together with their corresponding hypobranchials all fused into one piece. It ends posteriorly in an elongate, tapering median process.

Hypobranchials.—The pair corresponding to the first arch are represented by the lateral prominences (hbr. 1) on the posterior border of the basihyal. The second pair (hbr. 2) are flat and broad anteriorly, where they overlie the expanded part of the lower ends of the first ceratobranchials. They are somewhat thin there, and on the posterior edge are united by ligament to their corresponding ceratobranchials. Towards their posterior extremities they gradually taper and they are united to the second basibranchial. The third pair (hbr. 3) is essentially similar in shape to the second pair, the articulations being with the corresponding ceratobranchials and basibranchial. The fourth pair (hbr. 4) is more rounded than the second and third, and each hypobranchial has a bend in it so that the lateral part stands out at right angles to the axial portion. The cartilages forming this pair are fused in the median line, and are closely united by ligament with the large posterior basibranchial. In another example they are not fused with each other, but are closely and firmly attached together by ligament (fig. 6). The fifth pair is represented by rather prominent lateral processes (*hbr.* 5) which lie close to the anterior end of the large basibranchial. The sixth pair is also represented by lateral processes, not so pronounced, however, as the fifth pair.

Ceratobranchials.—I have little to add here to Garman's description, except to say that all—excluding the sixth—have a forward bend at their lower extremities, which brings these parts parallel with the median horizontal axis. The first and second pairs are curiously expanded also in this region, having an almost bilobate appearance. The posterior part of the expansion is rounded and underlies the expanded part of the following hypobranchials.

The sixth pair is very massive and on its anterior ventral border each has a thin, almost wing-like portion, which Fürbringer considers as the representative of the branchial rays of this arch. There is nothing of note in the epi- and pharyngo-branchials of the first five arches. In the case of the sixth, however, it is probable that only the epibranchial is present; the pharyngobranchial being perhaps incorporated with it. It has a peculiar shape, quite different from the slender, tapering bar figured by At its point of attachment to the distal end of the Garman. ceratobranchial it has an irregular outline. It next narrows somewhat, and then carries a small process on its inner concave border. The outer edge is convex and the whole piece gradually tapers to a rounded end, which is anteriorly and inwardly directed.

Seventh vestigial arch.—This is not present in the specimen which serves for the description of most of this paper, unless it be that it is represented by a pair of rather sharp ridges on the ventral side of the last basibranchial at the proximal ends of the sixth ceratobranchials. In the case, however, of the large female specimen it is present, and takes the form of a pair of small segmental, tapering pieces (v.b.a. 7) lying on the ventral side of the last basibranchial at the bases of the sixth ceratobranchials.

Each arch consists of two small pieces of cartilage united by connective tissue fibres to the surrounding parts. The more anterior portion in each is rather irregular in outline and on its posterior border carries a second slender, tapering portion. Fürbringer (6), who was the first to describe this very interesting vestige, merely speaks of it as a small piece of cartilage, and his figure gives no adequate idea of its structure and disposition relative to the surrounding parts.

As a matter of fact, it is very variable in structure; for that described by Hawkes (17) was made up of four small pieces on

one side and two on the other, lying close to the ceratobranchial of the sixth arch on the posterior side near to the median extremity.

## e. Branchial Rays.

These are thin, tapering rods of cartilage lying embedded in the interbranchial septa, a little closer to the inner surfaces of the latter than to the outer. Proximally they are applied to the posterior sides of the branchial arches, and distally they project somewhat beyond the margins of the interbranchial septa, to which they thus give a crenulate appearance.

One or two cases were observed in which two rays appeared to be fused proximally, apparently having a common origin. In another case two rays which had separate origins fused, and became produced so as to form one ray.

The greatest number of rays occurs on the hyoid arch, and as we proceed posteriorly the number gradually decreases for the six branchial arches, though subject to some variation. The sixth arch carries no distinct rod-like rays, but a thin laminate portion (l.p.) is found on the anterior ventral edge of the ceratobranchial. This, as previously mentioned, is regarded by Fürbringer as the representative of the branchial rays fused with the ceratobranchial. Whether this is the case or not, appears to me to be an open question. This lamina may be merely a thin extension of the ceratobranchial. Again, there seems to be no particular reason why the original branchial rays-if such were present-should have fused into a common lamina and have become firmly attached to the arch. As a rule, it appears, branchial rays are not met with on the last arch in Selachians, and why this portion should be looked upon as their representative in Chlamydoselachus it is somewhat difficult to understand. The first series of numbers in the following tables is from the complete male specimen; the second is from the large female. Both right and left sides are given.

Male.				R.	L.
Hyoid a	rch .			28	26
First bra	anchia	l arcł	1	18	17
Second	>>	22		16	17
Third	,,	77		14	14
Fourth	,,	22		13	14
Fifth	33	22		10	9

27

19 16

14

12

1.0

9

#### Female. Hyoid arch 25 First branchial arch ..... 19 Second ,, ..... 14 27 Third 15 37 " Fourth 14 .....

,, .....

37

,,

,,

Fifth

1910.]

## f. The Spiracle.

The external opening of the left spiracle is an obliquely placed slit on the postero-dorso-lateral surface of the head, measuring about one centimetre in length. The right one is about one-half this length. On removing the skin and carefully dissecting away the underlying spongy cutis which covers the jaw-muscles, it is seen that the lumen of the spiracle passes down into the oral cavity between the hyomandibular and the mandibular cartilages. Just inside the external opening, the cavity becomes enlarged and a short cæcal diverticulum is given off anteriorly. This is overlaid by the levator maxillæ muscle whose disposition has already been described. The cæcum extends as far forward as the anterior knob of the proximal end of the hyomandibular, which projects from the articular depression on the auditory capsule. It is not attached to the hyomandibular, but is separated from it by the hyoidean branch of the seventh nerve, which passes just internal and ventral to it. In all probability it is homologous with the more extensive cæca mentioned by Ridewood (27), which have been described in other Selachians by Müller and Van Bemmelen. In Scyllium, for example, the cæcum extends inwards over the hyomandibular and becomes firmly attached to the wall of the auditory capsule, being in some way concerned with the function of hearing. A similar cæcum is found in Heptanchus, so that here we have another point in which Chlamydoselachus differs from this member of the Notidanidæ. The pseudobranch in each spiracle consists of about ten short ridges, which lie on the anterior outer wall just inside the external aperture. In the Notidanidæ the pseudobranchs are said to be better developed than in any of the Selachians, so that in this respect we find Chlamydoselachus presenting a small difference from Hexanchus and Heptanchus.

# g. Features of Specialization and Comparison with Notidanidæ.

Perhaps the most important point in regard to the specialization of the skull of Chlamydoselachus is to be seen in the extreme length and mobility of the jaws. These are exceptionally long, extending from the anterior, almost terminal mouth to a point well behind the posterior limit of the cranium. This extension is remarkable; in fact, one quarter of the total length of the jaws is found in this region, and it is this feature, connected with the exceptional length of the hyomandibular, which gives the jaws their great mobility. Indeed, their disposition relative to the cranium is quite different from that found in any other Selachian whose skull I have been able to examine or to see a figure of. It resembles nothing among the Vertebrates so much, perhaps, as the general disposition of the jaws in certain of the Ophidia. ln this respect also Chlamydoselachus presents a striking difference from the two genera of the Notidanidæ. In both Hexanchus and Heptanchus the mouth is ventral and is situated far back. The

suspension of the jaws is amphistylic, and the palatoquadrate cartilages have a postorbital articulation with the cranium. Moreover, the extension of the jaws posterior to the cranium is but very slight.

### IV. THE MEMBRANOUS LABYRINTH. (Plate XLIII, figs. 7 & 8.)

The organ of the right side of the head has been worked out by dissecting away the surrounding cartilage, and forms the basis of the following account.

On removing the skin from the dorsal surface of the cranium it is seen that the parietal fossa is rather deep and possesses four apertures, two on either side of the median longitudinal line. One of these apertures, the anterior, is small, and transmits the ductus endolymphaticus. The posterior is larger and is closed with soft subcutaneous tissue. It is an opening into the perilymph cavity surrounding the posterior vertical canal, and seems to correspond to the tympanic aperture which Howes (19) described in *Raia*. Before proceeding further, I may mention that in this account I am following the nomenclature used by Stewart (30), which differs somewhat from that used by Retzius (26) in his great monograph.

The ductus endolymphaticus, on emerging from its cranial foramen, soon expands into the saccus endolymphaticus. The latter lies partly in the parietal fossa and is partly attached to the under surface of the skin covering this region. It is fairly regular in shape, somewhat rounded on its anterior surface, and extends posteriorly in a slightly outward direction, gradually becoming attenuated until it reaches its external aperture, which is quite small. Internally the ductus endolymphaticus leads into the sacculus. This is not rounded, but is laterally flattened, and gives off at its postero-inferior end the lagena in the form of a simple czecum.

The *utriculus* in this species is like that in other Elasmobranchs, being divided into two portions, anterior and posterior, which do not communicate directly with each other, but indirectly through the sacculus.

The anterior utricle is rather laterally compressed and gives off the anterior canal dorsally. The latter curves forward and slightly outward, and describes almost a semicircle in its course, expanding at its lower end into the anterior ampulla, which then opens by a wide portion into the lower end of the utricle again.

The recessus utriculi is a somewhat spherical structure on the inferior and outer border of the anterior utricle. It communicates with the latter by means of a slit-like aperture just below that leading into the *ampulla externus*. The anterior utricle does not open directly into the sacculus, but communicates indirectly with it through the recessus utriculi, which opens into the sacculus by means of a rounded aperture on the postero-dorsal side of the recessus.

[Mar. 15,

Arising from the dorsal end of the anterior utricle, and proceeding in a posterior and outward direction, is the *external canal*, which bends downward and comes to lie in an almost horizontal position. At its anterior end it is slightly elevated and expands into the *ampulla externus*, which communicates with the anterior utricle again by means of a short canal which rests on the upper side of the recessus utriculi, but does not open directly into it.

The *posterior utricle*, which is situated more internally than the rest of the labyrinth, is somewhat cylindrical in shape and is slightly curved upon itself. It communicates directly with the sacculus by means of a short, almost vertical canal, the *ductus utriculo saccularis posterior*. Arising from its dorsal end is the *posterior canal*, which curves outward and downward, and then expands into the *posterior ampulla*, which opens into the lower end of the utricle again.

All three canals, anterior and posterior vertical and external horizontal, are not rounded in section, but are markedly flattened, so that their height is equal to about twice their width. The external canal in its almost horizontal position lies with its compressed sides in the horizontal plane.

## Nerve-Supply.

The sensory areas of the membranous labyrinth are supplied by branches of the eighth cranial nerve.

After passing from the brain through its foramen, the nerve breaks up into a number of ramuli which supply their particular regions.

The *ramulus ampulla anterior* is a rather fine branch which extends from the main nerve-trunk to the anterior ampulla, lying chiefly on the outer side of the lower portion of the anterior utricle.

Arising next from the main trunk are two ramuli, which appear to have a common origin. These are the ramulus recessus utriculi and the ramulus ampulla externus. Both curve under the recessus utriculi and come to lie on its outer surface, the ramulus ampulla externus proceeding upward on to the external ampulla, where it supplies the two rounded cristae. The main portion of the nerve now goes on to form the ramuli sacculi. It first gives rise to a flattened branch which extends upward and follows the inner anterior border of the sacculus, thus forming The rest of the nerve proceeds in an one ramulus sacculus. almost horizontal direction and lies on the inner surface of the sacculus, forming the main ramulus sacculus. This gives off fine branches on its lower side which supply the maculæ of the sacculus. Arising from its posterior end are three fine branches: a lower one, the ramulus lagena. supplying the maculæ of the lagena; a median one, the ramulus ampulla posterior, lying chiefly on the inner surface of the posterior utricle and supplying the 1910.]

posterior ampulla; and an upper one, the *ramulus neglectus*, which curves upward toward the ductus utriculo saccularis posterior.

In structure and in the distribution of the nerve-supply the membranous labyrinth of *Chlamydoselachus* resembles rather closely that of *Notidanus* (*Hexanchus*) griseus figured by Stewart (30).

### V. VERTEBRAL COLUMN. (Plates XLIII.-XLV. figs. 9-17.)

The notochord is persistent, and reaches from the pituitary fossa in the basis cranii to the extreme tip of the long tapering tail. There is an elastic supradorsal longitudinal ligament which extends from the back of the cranium to a point just posterior to the dorsal fin, where the dorsal supports of the caudal fin commence. The number of vertebræ, as determined by neuromeres, is one hundred and twelve, and this number includes the irregular region at the extreme tip of the tail—to be dealt with in detail later. In determining this number, I have counted the ventral root foramina of the spinal nerves carried by the basidorsals, as these are larger than the dorsal root foramina. Moreover, the first foramen at the anterior end of the column is a ventral one. The vertebral elements present, named according to Gadow's (9) nomenclature, are as follows :---

*Dorsalia*: basidorsals, interdorsals, and suprabasidorsals, the last-mentioned being segmented off from the apices of the basidorsals. The dorsal radial supports of the caudal fin I do not consider as dorso-spinalia, because at their commencement anteriorly they are not always continuous with the neural arches, and, moreover, there is as much evidence to show that in general they originate independently of the vertebral column as there is in favour of their being portions segmented off from the dorsalia below them.

*Ventralia*: basiventrals, interventrals, ribs, and hæmal arches, and hæmal spines in the caudal region.

I have been unable to find the calcifications which Garman mentions as occurring in the mouths of the foramina for the spinal nerves. No trace of them can be detected even after carefully cleaning away the connective tissue which closely invests the vertebral column. In fact, it would be somewhat surprising if such calcifications were present, considering the small amount of calcareous secretion found in the skeleton at all.

It is perhaps worthy of note that, in the largest specimen examined, the vertebral column over the abdomen was not straight, but was contorted so as to have an undulating outline in the horizontal plane. Whether this was due to abnormal growth or to the action of the preservative I do not know, but I am inclined to the latter view.

In connection with the formation of centra, my investigations have revealed a number of points which Garman did not observe, and for this reason my account will be somewhat full. For purposes of description I have divided the column into four regions, 1, 2, 3, and 4, which are quite arbitrary, and, though not corresponding exactly with any recognized divisions of the body. yet may roughly be described as cephalic, trunk, main caudal and terminal caudal regions. My reason for doing so is, that to treat of the whole length of the column in a continuous description would mean a needless repetition of words, thus tending to make the meaning obscure. The regions are as follows :---1. Anterior cephalic portion extending for about twelve centimetres behind the skull. 2. The region extending from the posterior end of 1, over the abdomen and reaching to the level of the cloaca; what may conveniently be termed the "trunk region." 3. The main caudal region extending from the posterior end of 2 to a point about eleven centimetres from the tip of the tail. 4. The last eleven centimetres of the tail, terminal caudal region.

### h. Description of Regions 1, 2, 3, and 4.

The vertebral column is fused to the cranium quite firmly, so that but slight articulation is possible between the two. In this particular region of the column, viz. 1, there are regular vertebral constrictions of the notochord in the form of ring-like thickenings of the chordal sheath (fig. 9). This figure represents a view of a median, vertical, longitudinal section. It can be easily made out from this that each constriction occurs beneath a basidorsal, and also that the majority of the constrictions are well calcified. This particular point is of considerable interest, and is here fully dealt with. The first five constrictions-counting from the leftare calcified regularly, so that each centrum is typically cyclospondylic, being in the form of a short cylinder pinched in round the middle. The calcified areas thus present the appearance of two V's placed point to point. The sixth centrum has a calcified V above, but below, the calcification is irregular, being represented by only a small patch of calcareous secretion. The seventh is regular above, but below, the V is calcified all over. Eight, nine, and ten are also regular above and below, except that the lower V is larger in each case than the upper one, the latter in the tenth being very small. Constrictions are visible beneath basidorsals eleven, twelve, and thirteen, but no calcified areas are apparent in these cases, although, externally, the notochord shows definite calcified bands in the case of eleven and twelve. With these two, then, it is evident that calcification has not proceeded as far inward as in the more anterior ones. It also reveals the fact that the process of the deposition of calcareous salts begins on the outside of each constriction, and gradually proceeds towards the interior. Constrictions eleven and twelve may be looked upon, therefore, as being in a state of semi-calcification, whilst thirteen is merely a constriction of the chordal sheath, in which calcification has not commenced. The intervertebral

554

spaces are filled with soft notochordal tissue, and there are no secondary calcifications in these areas.

For comparative purposes I have thought it worth while to give a drawing (fig. 10) of a corresponding anterior region from another and larger specimen. In this there are seen eleven definitely calcified cyclospondylic centra, which gradually increase in width as we proceed from left to right. Each one is in the form of two V's placed point to point, and, moreover, corresponds exactly in position with a calcified band on the exterior of the notochord. It is worthy of note also that the soft notochordal tissue gradually becomes obliterated from the intervertebral spaces as we approach the skull, so that in the space between the first centrum and the cranium soft tissue is not present at all. The larger, more definite, and regular calcifications of the centra in the larger specimen are of considerable interest because they seem to indicate-as will be shown in another region of the vertebral column-that the extent to which calcification takes place depends upon the age of the specimen, for apparently the size depends upon the age. The older the specimen the more definitely and regularly calcified are the regions where calcification may occur. Garman mentions this region, and says that there are vertebral constrictions which are somewhat calcified, but he does not state how far this condition obtains, and his figure of a longitudinal vertical section taken in this region is very indefinite. The calcified areas are represented as being of irregular shape, much more rounded than those which I have found. They are also continuous with one another, whereas those which I have found are quite discontinuous.

Region 2.—The "trunk region" is the longest of all, and shows the least differentiation of the notochord. The dorsalia are represented by basidorsals and interdorsals, triangular in outline, suprabasidorsals segmented off from the apices of the basidorsals as small wedge-shaped pieces. The ventralia are represented by basiventrals, somewhat rectangular in outline, and rounded interventrals. The latter are comparatively small, and gradually decrease in size as we proceed posteriorly. The notochord is of uniform diameter, and shows slight but unmistakable signs of segmentation; each segment corresponding exactly with a basidorsal above and a basiventral below. The segmentation is shown by a difference in the appearance of the chordal sheath along lines corresponding in position to the ends of the basidorsals. At these points there appear to be narrow rings or annulations of the notochord as shown in fig. 11. In a view of the cut surface of a vertical longitudinal section of a portion from this region, no apparent constrictions of the notochord are found to correspond with the external segmentation of the chordal sheath. The interior of the chord presents a fairly uniform appearance, as was noted by Garman. If, however, a horizontal longitudinal section be made of the notochord, a regular sequence of constrictions of the chordal sheath is at once

apparent. Each of these occurs beneath a basidorsal, and extends between two consecutive segmentation marks on the exterior of the chordal sheath. Each takes the form of a bulging inward of the sheath, so that a slightly pinched-in cylinder is formed.

The regions described thus far are typically monospondylic, *i.e.* each neuromere is made up of one of each of the vertebral elements, one basidorsal, one interdorsal, one suprabasidorsal, one basiventral, and one interventral The foramina for the spinal nerves do not occur between the dorsalia, but are actual perforations of the basidorsals and interdorsals. In the monospondylic regions each basidorsal transmits a foramen for a ventral root and each interdorsal one for a dorsal root. The ventral root foramina are larger than the dorsal ones.

*Ribs.* These are small, thin, cartilaginous pieces segmented off from the basiventrals, with which they are continuous. They occur in regions 1 and 2, and extend from the eighth to the sixtyfourth neuromeres inclusive. At their posterior end they reach a point on the vertebral column a short distance anterior to the level of the cloaca, where they terminate abruptly, having apparently diminished but very little in size. More posterior to this point the basiventrals begin to grow downward, and gradually assume the form of wedge-shaped pieces which afterwards fuse beneath the hæmal canal and thus give rise to the hæmal spines.

Region 3.—At the seventieth neuromere we get the transition from the monospondylic to the diplospondylic condition taking place (see fig. 12). As represented in the figure, the latter condition appears to be brought about by the segmenting off of a small basidorsal from the anterior side of a typical monospondylous one. By this means each single large basidorsal gives rise to two smaller ones, and between these there is inserted a small interdorsal. The small basidorsals have narrow suprabasidorsals segmented off from their apices as thin wedge-shaped pieces. A ventral root foramen perforates the posterior one of each pair of diplospondylous basidorsals, whilst the succeeding interdorsal transmits a dorsal root foramen. In this way we have the typical diplospondylic condition of vertebræ brought about, and this arrangement obtains to a point about eleven centimetres from the tip of the tail. At the seventy-second neuromere, as shown in fig. 12, we find the monospondylic condition again occurring, apparently as a reversion to the more primitive stage in development. Instead of finding two of each of the arcualia we only have a single large basidorsal with a ventral root foramen near its posterior edge, followed by a single large interdorsal. However, on the lower side of the notochord there are two basiventrals and interventrals, thus indicating that although the dorsalia have not been segmented into the double condition, yet this has occurred in the ventralia. This single neuromere is of interest, because it seems to indicate that the diplospondylic condition is the secondary one, arising by segmentation of the parts which go to form the more primitive monospondylic condition.

It can be seen from fig. 13 that in this diplospondylic region we have an alternation of imperforate and perforate basidorsals, between which occur the perforate and imperforate interdorsals. On the ventral side of the notochord we have a similar segmentation of the ventralia. The notochord in this region has a segmented appearance, which is brought about by the occurrence of bands of cartilage round it. These bands are in reality extensions of the dorsal and ventral arcualia—basidorsals and basiventrals—round the chordal sheath, and they alternate regularly with spaces in which the sheath is naked. They are found in the trunk region as well, only there each cartilaginous band is very thin, and is only recognizable in microscopic sections.

In the main caudal region, however, the bands are much more pronounced in growth. Here also there is a marked difference in the relative size of the two kinds of basidorsals. The imperforate ones are larger than the perforate, and this difference in size obtains especially where the caudal fin is deepest. As we proceed towards the tip of the tail the dorsalia gradually become more nearly equal in size until at a point just anterior to where they lose their identity, they are quite equal.

Perhaps the most interesting feature, however, of the skeleton in this particular region is that which is found from a point level with the posterior end of the anal fin to within a short distance of the tip of the tail. Here we find definite calcified rings round the chordal sheath which correspond in position to the basidorsals above and lie internal to the cartilaginous bands just mentioned. They are shown in fig. 13, where they appear as unshaded bands on the notochord extending between a large imperforate basidorsal above and the corresponding basiventral below. There is also an indication in the figure of a band beneath a perforate basidorsal and this, as it stands, may be somewhat misleading, appearing as if it were somewhat exceptional. This, however, is not the case, as only a short distance posterior to the portion figured the calcified rings become as well marked beneath the perforate basidorsals as beneath the imperforate ones. Fig. 14 represents a longitudinal vertical section of fig. 13. It is at once apparent from this that internal to each broad calcified band, *i. e.* beneath each imperforate basidorsal, we have a constriction of the chordal sheath in the form of an incipient centrum, the calcification extending into it and lending it additional strength. Beneath each perforate basidorsal also there is a very slight constriction of the chordal sheath without any trace of calcification.

The points just dealt with are shown much more clearly in a portion of the vertebral column taken from the larger, and probably older, female specimen. In this the extensions of the arcualia are very pronouncedly developed in the main caudal region, those beneath the perforate basidorsals being quite well shown. Both the latter and the larger ones beneath imperforate basidorsals are ridged in surface view as shown in fig. 15 In a view of a longitudinal vertical section of this portion (fig. 16), it is at once evident that in this specimen the formation of centra has proceeded much farther than in the smaller and, doubtless, younger specimen. The constrictions beneath the imperforate basidorsals extend well towards the centre of the notochord, whilst those beneath the perforate basidorsals are quite well developed, being much larger and more sharply defined than the corresponding constrictions in the smaller specimen. In both large and small constrictions also calcification has taken place, so that rounded V's are shown in the sectional view.

In the caudal region, then, we have well-marked, incipient, cyclospondylic centra. Another point which is especially interesting is that the calcified rings become most strongly developed in that part of the notochord below which the ventral lobe of the caudal fin has its greatest depth. One would expect this to be the case when the occurrence of centra and calcified bands is considered from the point of view of the mechanical importance of this region. If the diplospondylic condition of the vertebral column is concerned, as Ridewood (28) suggests, with flexibility, then we have here double the number of parts capable of articulation with one another that we should have if the monospondylic condition obtained in its place. Since also, the greatest purchase on the water is obtained by the tail where the caudal tin is deepest, we should expect to find here not only flexibility provided for but also a provision for increased strength in the skeletal supporting tissue. This is indeed what we actually find, for, as pointed out above, the diplospondylic condition is found here and the incipient centra are most strongly developed and calcified over the deepest part of the caudal fin.

Region 4.—This short region is of particular interest, because it has not been figured and described before. The specimen which Garman figured had lost the extreme tip of the tail. Fig. 17 represents it natural size, and from this it is seen that the vertebral column is a gradually tapering structure which remains segmented up to the end, no wostyle being present. The notochord has but very slight growths of the arcualia round it, and in two parts it is slightly segmented externally. In the dorsalia at the commencement of the region can be recognized both basidorsals and interdorsals. Very soon, however, the distinction between them becomes lost and they apparently fuse with each other to form small, irregularly shaped pieces, which, towards the extreme tip, are rhomboidal in outline and are of varying lengths. The dorsal radial elements, which are borne on the dorsal side of the neural arches, are also of variable length. They do not correspond segmentally with the dorsalia, and as we approach the extreme tip of the tail they become comparatively long. The hæmal spines are the most regular in shape and occurrence, being, with one or two exceptions, of the same width up to the end of the tail.

The point of special interest in this region is the disposition

1910.]

of the nerve foramina, which perforate the dorsalia. Anterior to the portion figured, the caudal region is typically diplospondylic. as already described. The ventral foramina are, throughout the vertebral column, larger than the dorsal ones. At the commencement of the figure, on the left-hand side can be seen a basidorsal which carries a nerve foramen. The succeeding interdorsal is imperforate, the dorsal and ventral roots of the spinal nerve having apparently united or approximated very closely together so that one foramen will transmit both. This condition also holds for the succeeding spinal nerves. In counting the number of dorsal elements separating the foramina depicted in fig. 15, it is seen that between the first foramen and the following one there are two dorsal elements. Between the second and third there are also two; between third and fourth, three; between fourth and fifth, nine; between fifth and sixth, eleven; and between this and the end of the tail there are thirty elements without a single perforation. This arrangement of the foramina in relation to the number of dorsalia is obviously quite irregular, and so far from being in accord with Ridewood's (28) and Mayer's (22) contention that the terminal region of the vertebral column is monospondylic, it shows that in *Chlamydoselachus*, at any rate. the neural apertures are so irregular in arrangement that this particular region may quite well be termed 'heterospondylic.' The musculature of the region in question is very much reduced, and we should scarcely expect to find so perfect a nerve-supply as is found more anteriorly. Moreover, with the irregularity in the shape and size of the arcualia and their non-segmental arrangement relatively to one another, it is difficult to imagine how a monospondylic condition could obtain here.

It seemed desirable to ascertain in what relation the myomeres of the tail stand to the neuromeres. In order to do this the skin was taken off from the other side of the tail and posterior portion of the trunk, so as to reveal the myomeres with their separating myocommata. On examining the limits of the myomeres it was seen that each one in the trunk corresponds in extent with a monospondylic neuromere. In the main caudal region each myomere is equal in extent with a diplospondylic neuromere. A determination was next made of the number of myomeres from the beginning of the diplospondylic region to the point where the distinction between the separate myocommata is lost, i. e. within five centimetres of the extreme tip of the tail. This number is forty-two. The number of neuromeres was next determined for the same region, and this also is forty-two. Thus the number of myomeres and neuromeres is the same in the tail, and each irregular or heterospondylic neuromere of region "4" has its corresponding myomere.

The number of neuromeres for the side of the tail on which the myomeres were counted was next determined. After carefully removing the muscular tissue, the spinal nerves were left, and by examining these through a dissecting microscope their

[Mar. 15,

number and distribution could be determined. The relation of their foramina to the dorsalia presents a considerable difference from the condition found on the other side of the tail. The total number of neuromeres for the region in question is the same for both sides, viz. forty-two; but instead of the irregularly-disposed foramina being separated by dorsal elements arranged in the order of the numbers, 2, 2, 3, 9, and 11, we find the following numbers of dorsalia separating them, 1, 2, 2, 2, and 14. From this it can be seen that the regular diplospondylic condition has proceeded one neuromere more posterior on this side than on the other, and that the following three are also more regular than the corresponding three of the other side. But there is no indication of a return to the monospondylic condition. This very interesting condition of heterospondyly is one which, so far as I have been able to ascertain, has not been described for any other Selachian fish.

### i. Summary of special features and comparison with Notidanidæ.

In summarizing the leading characteristics of the vertebral column of Chlamydoselachus, the following points may be mentioned :- First, the variety which it exhibits in the formation of At the extreme anterior end the constrictions form centra. cyclospondylic well-calcified centra. These may be followed by smaller constrictions in a semi-calcified condition. In the trunkregion are found the slightly constricted cylinders of the notochord, representing the lowest of all the stages in centra-formation. The main caudal region is characterized by the occurrence in it of constrictions of two sizes, the larger more calcified ones lying beneath the imperforate basidorsals, and the smaller less calcified ones lying beneath the perforate basidorsals. This difference in size gradually becomes lost as we proceed towards the tip of the tail, the constrictions becoming equal in size concurrently with the equalization in the size of the imperforate and perforate basidorsals. This particular point of the occurrence of centra in the tail-region is deserving of special emphasis, inasmuch as three recent text-books of zoology give the uniform character of the notochord and absence of centra in this region as a diagnostic feature of the Chlamydoselachidæ. The very pronounced growth of the basidorsals and basiventrals around the chordal sheath in the main caudal region is also very noteworthy. The great length of the diplospondylic region is of considerable interest, extending as it does through thirty-eight neuromeres, viz., from seventy to one-hundred and eight. The heterospondylic portion of the tip of the tail is, so far as I am aware, unique in Selachians.

The points at which the calcified centra occur is perhaps deserving of some mention. It seems that they are found where there are the greatest demands made for strength. At the anterior end, combined with the fusion of the vertebral column

560

### 1910.]

to the cranium, they give a rigidity to the supporting elements which is of service no doubt in enabling the fish to cleave the water. In the caudal region they meet the demand for increased strength caused by the purchase which the caudal fin obtains upon the water.

Compared with Hexanchus the vertebral column of Chlamydoselachus must be regarded. I think, as showing more specialized characters. In the former the notochord is simply constricted by annular thickenings of the cartilaginous sheath, no calcifications being present. The vertebral column of Heptanchus, however, is on the whole more specialized than that of Chlamydoselachus, for although the double-cone arrangement is not so pronounced at the anterior end as in Chlamydoselachus, yet the notochord is constricted vertebrally by a series of calcified rings which assume more and more the form of double cones towards the tail. And, moreover, in the caudal region secondary calcifications may give rise to a number of short rays radiating out from the centre of the double cones.

## VI. PECTORAL GIRDLE AND FINS. (Plate XLV. fig. 18.)

Pectoral girdle.--I have nothing to add to the account of the girdle given by Garman (10. pp. 13, 14), except to say that my observations, made on three girdles, agree with his description and figure, neglecting of course a few triffing details due no doubt to individual variations.

Pectoral fins.—In regard to the pectoral fins there are certain rather important differences between the account and figure given by Garman and the observations which I have made on three pairs of fins. The articulation of the fin with the coracoid is unibasal, and the articular surface of the mesoptervgium is about twice as large as that of the propterygium.

The propterygium is small, triangular in outline, and has a hollow articular surface. It carries no radials.

The *mesopterygium* is moderately large, is irregular in shape, resembling somewhat a truncated triangle, not being nearly so triangular as that figured by Garman. It carries radials on its posterior edge which show various degrees of fusion.

The metapterygium is an elongate, laterally compressed cartilage, carrying a large number of radials. It has a rounded dorsal ridge and gradually curves outward, not being practically straight as represented by Garman. Usually it is bisegmental, but in this respect it presents some interesting variations, for in two fins which I have examined it is trisegmental. In the former condition the proximal segment is the longer one and is more laterally compressed than the distal segment. The trisegmental condition is represented in two ways; first by the addition of a small proximal segment articulating with the coracoid, similar to that figured by Braus (3), and second, by the intercalation of a short segment between the normal proximal and distal segments. 36

PROC. ZOOL. Soc.-1910, No. XXXVI.